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COMPARATIVE RAPIDITY OF EVOLUTION IN VARIOUS PLANT TYPES

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DURING the course of evolutionary development among the higher plants certain groups have evidently altered with such exceeding slowness as to retain their ancient constitution practically intact for very long periods; whereas others, by their more rapid accumulation of heritable variations, have during the same time undergone far-reaching changes and become developed into new and radically dissimilar types. These differences in the rate of evolution are apparently due in part to differences in mutability, in the extent to which hybridization has occurred, in the degree of diversity presented by the environment or in the keenness of the struggle which is waged for survival. The purpose of the present paper is to call attention to still another factor which seems to be of much importance in determining the rapidity of evolutionary change among plants, namely the length of the generation or period from seed to seed.

The time necessary for the attainment of reproductive maturity among plants is definitely correlated with the growth-type to which a species conforms. Trees are very slow to mature, some arriving at an age of eighty years or more before their first flowering time and very few indeed, under natural conditions, fruiting before the tenth season. The scanty available observations seem to indicate that the average period from seed to seed in arborescent forms is in the vicinity of twenty years. Among shrubs the generations are decidedly shorter, varying usually from three to ten years. The herb is the most rapidly maturing of all, a single year sufficing to develop seed in an annual and but two (rarely more) in a biennial or perennial. Most herbaceous species will thus have from fifty to one hundred generations a century, most shrubby ones from ten to thirty and most trees only four or five. The degree of variability and other factors being equal, therefore, one would expect changes to accumulate much more rapidly and evolutionary progress consequently to be much faster among herbs than among woody plants. Is there evidence that this is actually the case?

In an attempt to obtain such evidence an analysis as to growth-habit was first made of the endemic portion of the floras of several regions. Upon the biological isolation of an area the new varieties, species and genera of plants which gradually take their origin in its flora are necessarily limited in their distribution to the region in question, or are "endemic" in it; and these local types will evidently be produced first and in greatest abundance by those elements in the flora which are changing most rapidly. Consequently that particular growth type which is found to predominate among such endemic forms may justly be regarded as the one whose members are undergoing the most rapid alteration. In an analysis of the endemic element in any flora, however, caution must be used to distinguish carefully two radically different types of endemic plants: those under discussion, which were local in origin and have never spread abroad; as contrasted with those which owe their present localization rather to the fact that they are isolated survivors of genera or species at one time much more widely distributed. The former category, which we may call the "indigenous" endemics, will evidently represent a new element in the flora; the latter, or "relict" endemics, a very old one. It is not always easy to separate sharply these two types in a given flora, but species, and especially genera, which stand apart and possess no near relatives in the region are, in most cases, at least, evidently to be looked upon as relicts; whereas in a group of species or genera the members of which are numerous and closely related one to another we doubtless behold a body of plants undergoing evolutionary development on the spot.

It is an analysis only of the latter type which is of significance for the present problem.

The genera of dicotyledons endemic[1] in temperate North America (Canada, the United States and northern Mexico) and in Europe (inclusive of the entire Mediterranean floral province) were studied in this connection. 400 genera were recorded as being endemic or essentially so in temperate North America. In this imposing array of types which are limited in their distribution to this region approximately 130 stand in isolated positions in the flora, being quite without near relatives, and are presumably "relicts." To this category belong *Carya, Planera, Maclura, Garrya, Sassafras, Xanthorrhiza, Baptisia, Nemopanthus, Ceanothus, Dirca, Dionaea, Hudsonia, Rhexia, Ptelea, Decodon, Houstonia, Symphoricarpos* and many other familiar plants. That these now exclusively American genera were indeed at one time much more widely distributed is indicated by the fact that many of them are found as fossils in Europe and Asia to-day. They undoubtedly represent a very ancient element in the flora. The most noteworthy feature of these "relicts" is that they include practically all the genera of *woody* plants endemic to this region, the typically American trees and shrubs.

Such ancient and isolated relicts, however, compose but a minority of the endemic genera. The remainder evidently belong to the other category and owe their endemism rather to the fact that they have been developed in America and have never spread beyond its borders. It is such endemic types which are of interest to our problem. That they are actually of local origin is rendered probable by their occurrence in groups of closely related genera (many of which are rich in species) each group presumably representing a separate center of evolutionary development and the nucleus for a new subfamily. There are over sixty such groups of allied genera in the endemic flora of North America. Notable among these are the alliances centering about *Eriogonum* in the Polygonaceæ; about *Streptanthus* and about *Lesquerella* in the Cruciferæ; about *Eschscholtzia* in the Papaveraceæ; about *Heuchera* in the Saxifragaceæ; about *Cercocarpus* in the Rosaceæ; about *Godetia* in the Onagraceæ; about *Cymopterus* in the Umbelliferæ; about *Pterospora* in the Pirolaceæ; about *Cryptanthe* in the Boraginaceæ; about *Trichostema* and about *Agastache* in the Labiatæ; about *Pentastemon* and about *Castilleja* in the Scrophulariaceæ, and about *Brickellia,* about *Solidago,* about *Boltonia,* about *Silphium,* about *Rudbeckia,* about *Hemizonia,* about *Baeria,* and about *Microseris* in the Compositæ. Most of these groups of genera have their center of distribution in the southwestern United States or in northern Mexico. The great majority of endemic genera in Europe are also evidently "indigenous" rather than "relict" in character. Centering chiefly in the Mediterranean region there are seventy or more groups of closely allied genera, notable among which are the alliances dominated by *Dianthus, Brassica, Alyssum, Lotus, Scandix, Asperula, Scabiosa, Anchusa, Anthemis, Carduus,* and *Cichorium.*

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[1] Genera in which 90 per cent. of the species or more are confined to the region in question were considered as endemic there. Genera rather than species were studied since they represent a greater degree of evolutionary change; and since endemism among species is so nearly universal on the two continents as to make its investigation of little value.

These "indigenous" endemic genera constitute a very characteristic and important part of the present-day flora of North America and Europe. Had they existed in anything like their present numbers and importance at the period when an easy exchange of plants was possible between the two northern continents, it is hard to believe that they would not now be well represented in the floras of both; particularly since herbs, of which we shall see these genera to be almost exclusively composed, tend more quickly than any other plant type to loose their endemic character because of the power to migrate rapidly and populate wide areas which is conferred by their ability to produce seed from seed in a single generation. This is well shown by the fact that in DeCandolle's famous list of 117 species, each of which at present occupies at least one half of the land area of the globe, there are none but herbaceous forms. Since we have cause to believe that communication between North America and Europe existed until well into the Tertiary, the supposition is altogether reasonable that the genera in question have undergone at least the greater part of their development and dispersal since that time; and that in contrast to the "relicts" and the non-endemic genera they represent an element of very recent development in the floras of the two regions.

It is noteworthy that these indigenous endemic genera are composed almost exclusively of herbaceous species, *Cercocarpus* and its allies among the Rosaceæ furnishing practically the only exception to the rule in America. If the conclusion is correct that such endemic types are the most recently developed members of a flora, this dominance of the herb among them constitutes excellent evidence that it is the herbaceous element which has indeed been undergoing the most rapid evolutionary change.

In striking contrast to the highly endemic and local character of so many of the north temperate genera of herbs is the wide geographical range almost universal among the woody types. Nearly all the tree genera of temperate North America exist to-day on some portion of the Eurasian continent or give evidence by fossils that they once did exist there. The whole study of endemism in its relation to growth forms presents us with the picture of a very slowly changing woody vegetation, one which since the separation of the two northern land masses has given rise to few or no generic types, but which has been accompanied by a rapidly developing herbaceous flora so quick to originate new forms that upon isolation it has produced not only a throng of local species, but even a goodly number of genera.[2]

Evidence of value in the present problem may also be derived from a study of the relationship of the members of the various growth forms and their distribution in the modern system of plant classification. During the history of the vegetable kingdom, the continual evolution of species, genera and families has been opposed by their continual extinction, for one cause or another. One would expect that those types in which evolution was proceeding most rapidly would occur in groups, usually rather large, of closely related species and genera, and that members of such groups which subsequently came to be isolated by the extinction of their allies would soon become centers of development and give rise again to new groups. Monotypes would consequently be rare among them. The more slowly evolving forms, on the other hand, would be able to repair the ravages of extinction much less rapidly and easily and would therefore tend to occupy more or less isolated positions in the system, frequently as monotypic genera or families.

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[2] The predominance of woody plants which is so pronounced in the endemic element of the floras of oceanic islands and of somewhat isolated continental areas in the south temperate zone, is evidently due to the fact that most of the herbaceous portion of the vegetation here has so recently arrived from its seat of origin in the great land areas of the north, that it has not yet had time to develop into endemic species and genera on a large scale.

To determine the distribution of herbs as contrasted with woody plants in the present scheme of classification an analysis was made of the dicotyledons in Engler and Prantl's "Naturliche Pflanzenfamilien," supplemented and brought up to date as far as possible by the seventh edition of Engler-Gilg's "Syllabus der Pflanzenfamilien." The figures obtained of course can not be regarded as exact, but they are at least definite enough to bring out certain general facts.

One hundred and eight thousand species of dicotyledons were counted, grouped in 6,840 genera and 238 families; 4,030 genera, comprising slightly over 50,000 species, were found to be composed entirely of woody plants, and 2,630 genera, with slightly under 40,000 species, entirely of herbs; 180 genera, containing over 18,000 species, included both woody and herbaceous members and were disregarded in the count.[3] The average number of species in the woody genera is therefore 12.5, in the herbaceous ones, 15. In their large genera (including 10 species or more) the two types are practically the same, there being an average of 45 species per genus in the former and 46 in the latter. This of course pulls the general averages together. The more scattering distribution of trees and shrubs, however, is made evident by the fact that of small genera (10 species or less) they possess 3,115, as compared with 1,890 for herbs.

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[3] If 90 per cent. of the species of a genus were woody, that genus was counted as "woody"; if 90 per cent. were herbaceous, it was counted as "herbaceous." "Mixed" genera include more than 10 per cent. of each type.

The two types are somewhat more diverse in the number of genera per family. In an analysis to determine this distribution, only land plants of normal growth-habit were considered. The Balanophoraceæ, Rafflesiaceæ, Hydnoraceæ, Lennoaceæ and Cynomoriaceæ were excluded as aberrant; and families characteristically aquatic were also omitted, since from their uniformity of environment or other reasons unknown they are notoriously poor in generic types. Two hundred and twenty-four families of dicotyledons enumerated in the seventh edition of Engler's "Syllabus" remain to be considered; 130 of these are exclusively woody, 60 have both woody and herbaceous members, and only 34 are exclusively herbaceous,[4] making it evident at a glance that woody plants have much the wider taxonomic distribution. In the 190 families which include trees and shrubs, there are just 4,000 genera, an average of 21 per family. In the 94 families which include herbs, there are 2,590 genera, an average of 27.5 per family. (The 180 "mixed" genera were left out in this count.) The fact that the bulk of genera in both are massed in a few large families again pulls the averages together; but the more scattering distribution of woody genera over a large number of small families is decidedly emphasized when we note that there are no less than 39 monogeneric families of trees and shrubs, but only 7 of herbs (exclusive of aquatics). Of families with 5 genera or less there are among woody plants 83, among herbs only 24. In number of species per family the difference between the two types is still more marked, for the 190 woody families include about 59,000 species, an average of 310; the 94 herbaceous families about 49,000 species, an average of 510.

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[4] Families like the Ranunculaceæ, Papaveraceæ, Crassulaceæ, Geraniaceæ and Umbelliferæ, which possess exceedingly few woody species, have been counted as strictly herbaceous; and others like the Sapindaceæ, Araliaceæ and Bignoniaceæ, in which there are very few herbs indeed, have been counted as strictly woody.

It is therefore evident that herbs tend to be massed in a comparatively few large genera and families. Among trees and shrubs, on the other hand, although the majority of species are also naturally in large, successful groups, there is a very much greater proportion of small genera and especially of small families, widely scattered throughout the whole taxonomic range, which have been isolated by the wholesale extinction of related forms and are apparently very slow to develop into larger aggregations. Such evidence as this, like that derived from a study of indigenous endemism, seems to indicate that the rate of evolution among herbs is decidedly higher than among woody forms.

There are doubtless numerous exceptions on both sides. *Cratægus, Eucalyptus, Acacia* and other genera of trees and shrubs appear to be rapidly developing new species, whatever the cause thereof may be; and many herbs, far from producing new forms, show every indication of being stationary or even of becoming extinct. These are both evidently exceptions to the general rule, however.

Of course these cases introduce the consideration of another factor, naturally thought of first in connection with rate of evolution among any organisms, namely, their comparative "variability," using the term in its broadest sense. To contrast members of the two growth types as a whole in this respect is necessarily very difficult, but an attempt was made to do so by comparing the proportion of varieties and named forms among the woody plants with that among the herbs in a number of floras. The results are shown in the table (p. 474).[5]

The proportion of varieties and forms is therefore practically the same among woody plants as it is among herbs, and if this is to be regarded as at all a criterion of variability, there is little to choose between the two growth

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[5] Dicotyledons only are considered.

	Species		Varieties and Forms	
	Woody	Herbaceous	Woody	Herbaceous
N. E. United States....	532 (23%)	1,748 (77%)	144 (31%)	322 (69%)
Ceylon................	1,123 (63%)	670 (37%)	165 (60%)	112 (40%)
Australia..............	3,970 (70%)	1,741 (30%)	752 (70%)	325 (30%)

forms. The greater plasticity probably belongs to the herb, owing to the larger independence of environment which its discontinuous existence allows. Brevity of life-cycle, however, rather than higher variability, is probably the cause of the more rapid rate of change exhibited by members of this type.

The conclusion that herbs have been evolved much more rapidly than trees or shrubs has certain important corollaries. There are at present approximately 2,600 genera of dicotyledonous herbs and 4,000 genera of woody plants. The much wider taxonomic range which we have noted in the latter type makes it probable that in extinct species and genera their numerical superiority is still greater. If herbs are thus decidedly fewer than woody plants in number of species and genera, but are nevertheless being produced at a much more rapid rate, it is highly probable that the herbaceous element in the flora of the world must have had a shorter evolutionary history than the woody one. This is in harmony with a considerable body of evidence derived from a study of the history, structure and distribution of the Angiosperms, which indicates that the most ancient members of the group were woody and that herbaceous vegetation has made its appearance in comparatively recent geological time.[6] The great steps in the evolution of the higher plants seem to have taken place while trees and shrubs were the dominant growth types, for all the important orders and the great majority of families are still composed wholly or in part of such plants. Herbs occur to-day in less than half the families of the dicotyledons, and although such a dominant portion of the vegetation in many regions, they seem to be of relatively recent appearance.

[6] Sinnott, E. W., and Bailey, I. W., "The Origin and Dispersal of Herbaceous Angiosperms," *Annals of Botany*, XXVIII, 1914, pp. 547–600.

A study of the comparative rate of evolution among the Angiosperms also throws a little light on the antiquity of this great group. Its fossil representatives have as yet failed to make their appearance in strata lower than the lowest Cretaceous, and it is commonly assumed that they had their origin at about that period. We have already noted the probability that they were represented at their inception only by woody forms. There is evidence that the herbaceous type, save perhaps as a negligible portion of the flora, did not arise till the early Tertiary, since which time its members have undergone practically their entire evolutionary development. As to the relative lengths of geological periods there is no very definite evidence, but authorities agree that the Mesozoic was of considerably longer duration than the Tertiary, a conservative estimate placing the former at about three times the length of the latter. Let us grant for purposes of argument that this is a reasonably close approach to the truth; and let us also assume that herbs have evolved at a rate averaging twice as great as that of woody plants, surely a moderate supposition. All the 2,600 exclusively herbaceous genera presumably developed as herbs; and there are 4,200 genera which contain woody plants and which probably originated as woody plants. Now if these 2,600 herbaceous genera have been developed since the beginning of the Tertiary, woody plants, producing new forms at half this rate, would during the same time have given rise, let us say, to 1,300 genera. To produce the other 2,900 woody genera (to say nothing of the hundreds which have become extinct) would require, assuming the same rate of evolution, another period twice as long as the Tertiary, thus thrusting back the origin of the Angiosperms to a date distant from the present thrice the length of the Tertiary. According to the estimate mentioned above, this would be about the beginning of the Jurassic. Of course this is all extremely hypothetical, but it serves to emphasize the probability that in order to have developed their great number and diversity of slowly changing woody forms, the Angiosperms must have been in the process of evolution for a period many times as long as that since the origin of herbs, evidently beginning at a date far earlier than that at which the first angiospermous fossils occur.

This conclusion is still further strengthened by other facts. The earliest fossil Angiosperms seem to have been trees, presumably the most slowly alterable type of all. Furthermore, whatever may have been the importance in recent times of hybridization through cross-fertilization by insects as a cause of accelerated evolution, this factor was evidently inoperative at the origin of the Angiosperms, since, according to Handlirsch, flower-loving insects did not make their appearance till the Tertiary. The specialized character and apparently high phylogenetic position of many of the earliest fossil Angiosperms also renders it highly probable that they were the product of a long evolutionary history.

Evidence from all sources therefore seems to agree that the origin of these higher seed plants took place at a time very much earlier than their paleontological record indicates. That they were not preserved as fossils in horizons lower than the Cretaceous is perhaps due to the fact that the earliest Angiosperms, as Professor Bailey and the writer have suggested,[7] appeared under essentially temperate climatic conditions, which in the Mesozoic were mainly confined to upland regions where fossilization would take place much less commonly than in lowlands. This apparent predilection of these primitive Angiosperms for an environment cooler than the tropical, together with what we have noted as to their high antiquity, suggest that the refrigeration of climate which took place in the Jurassic might have been a factor in their origin; and even tempts one to look farther back toward the epoch of markedly low temperatures subsequent to the close of the Paleozoic, which caused so many radical changes in the organic world, as perhaps the time when the angiospermous stock began to be differentiated from its gymnospermous ancestors.

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[7] Sinnott, E. W., and Bailey, I. W., "Foliar Evidence as to the Ancestry and Early Climatic Environment of the Angiosperms," *Amer. Jour. Bot.*, II, 1915, pp. 1–22.

We may point out, in conclusion, that a recognition of differences in the rate of evolution between various growth forms is evidently of importance in many problems concerned with the phylogeny, ecology or distribution of the higher plants. Upon the question, for example, as to whether the boreal species in the floras of southern South America and Australasia are of ancient or recent arrival there, some light is thrown by the fact that these species are almost all herbs. That so many members of a growth-form which is usually subject to rapid change still maintain specific identity with distant northern types argues strongly for their comparatively recent arrival in the south. A similar question is raised by Willis's studies of the flora of Ceylon.[8] He regards the endemic element here as one which is of local and recent origin and as much younger than the non-endemic element; but the fact that of the endemic species, by implication the ones which are changing the fastest, less than one fourth are herbs, whereas nearly one half of the non-endemic species belong to this growth-form, would suggest the opposite conclusion; for had this large body of herbs been in existence here for a very long period, as Willis supposes, we should have expected it to develop a relatively much greater body of endemic species. In such questions as this it should be borne in mind that evolution has not been a steady and uniform process among all forms, but that the decided differences between the various growth types in the rapidity with which they tend to accumulate heritable variations introduces a factor which it is always necessary to consider.

SUMMARY

1. The most recently evolved element in the floras of temperate North America and of Europe, as determined

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[8] Willis, J. C., "The Endemic Flora of Ceylon, with reference to Geographical Distribution and Evolution in General," *Phil. Trans., B,* CCVI, 1915, p. 307.

by a study of the indigenous endemic genera, is composed almost entirely of plants which are herbaceous in habit.

2. Herbs tend to be grouped in fewer and larger genera and families than woody plants.

3. It is therefore concluded that herbaceous plants, presumably because of the brevity of their life cycle and the rapid multiplication of generations consequent thereto, are in most cases undergoing evolutionary development much more rapidly than are trees and shrubs.

4. From this conclusion are drawn inferences as to the origin of the herbaceous habit and the antiquity of the Angiosperms.